Drivers of ecological and geomorphological patterns in the complex beach system

TUA NYLÉN

ACADEMIC DISSERTATION
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Abstract

The unique environmental setting of the land uplift coasts and advanced methods provide novel opportunities to analyse spatio-temporal environmental processes. The aim of this doctoral thesis is to expand on the understanding of the beach and adjacent dune field as a complex ecogeomorphic system. This system includes the abiotic environment, substrate and vegetation and the links between these components. Knowledge of the beach system is mainly based on descriptive research and studies focusing on its distinct components. Furthermore, the current ecogeomorphology research is centred on the landform-process-interaction treating vegetation as an invariable factor. Thus, general patterns and processes of beach systems are still insufficiently understood.

In this doctoral thesis, individual components of the ecogeomorphic system are analysed using appropriate modelling methods and homogeneous observational data that covers a large geographical area (60° N – 65° N). Thus, the robustness of existing geomorphological and ecological theories is assessed on the sandy coasts of the Baltic Sea in Finland. More specifically, the thesis aims at answering: (1) which abiotic, biotic and temporal factors are the main determinants of substrate (soil) and vegetation properties, (2) what are the effects of the main drivers on substrate and vegetation properties, (3) how temporal processes interact with main spatial drivers in determining species richness and (4) how these effects differ between species and functional groups representing different adaptive strategies?

Two advanced statistical methods are utilised to analyse the effects of multiple factors on substrate and vegetation. Boosted regression trees (BRT) efficiently model nonlinear relationships and interactions without *a priori* model specification. Generalised linear mixed models (GLMMs) take the effects of nested data structure and local environmental variability into account to clarify general relationships.

My results demonstrate that the textural substrate properties vary stronger between beaches than along local environmental gradients. Textural properties are largely determined by parent material and shore exposure to winds and waves. Due to weak earth surface processes, low-energy beaches are characterised by poorly sorted and coarse sediments. Organic matter is accumulated in litter layer and soil in sheltered places. Moreover, low-energy beaches provide favourable conditions for higher soil organic matter accumulation.

The relative contribution of time is lower than expected in substrate models but notable in vegetation models. In addition to time, disturbance, productivity and biotic interactions are the main determinants of vegetation properties. My results therefore highlight the role of biotic factors in shaping vegetation. The thesis demonstrates how the strong interplay of spatial and temporal processes controls species richness in land uplift beaches. While the patch size and connectivity of beach habitat have minor effects on total species richness, they strongly influence specialist species. Finally, the responses to all environmental drivers are specific to functional group and individual species. Thus, the mixed responses and interplay of drivers create the mosaic of vegeta-

tion assemblages.

The doctoral thesis contributes to understanding the components of the ecogeomorphic beach system by identifying the main drivers of substrate and vegetation. Particularly, I demonstrate the variety of ecologic responses and the importance of dominant species in shaping vegetation assemblages. The beach and adjacent dunes are considered as a continuous system instead of separate zones. Furthermore, the feasibility of extensive homogeneous datasets and advanced modelling methods are demonstrated in analysing beach processes. Thus, the thesis may serve as one step towards a more in-depth understanding of the complex beach system and provide new methodology for further research. This knowledge is vital to the conservation of beaches that are unique landscapes and considerably contribute to biodiversity but are subject to multiple land use pressures.

Acknowledgements

Miska Luoto and Pirjo Hellemaa supervised the study and contributed to the articles. I am grateful to them for the valuable support throughout the process. In addition to the supervisors, Peter le Roux contributed to one of the articles and taught me a great deal about scientific writing, academic English and the publishing process. My preliminary examiners, professors Anke Jentsch and Risto Kalliola, gave important feedback and advice on the manuscript of the summary.

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Contents

List of original publications

This thesis is based on the following publications:

I Nylén, T., Hellemaa, P., Luoto, M., 2015. Determinants of sediment properties and organic matter in beach and dune environments based on boosted regression trees. Earth Surface Processes and Landforms, doi: 10.1002/esp.3698.

II Nylén, T., le Roux, P.C., Luoto, M., 2013. Biotic interactions drive species occurrence and richness in dynamic beach environments. Plant Ecology 214, 1455–1466.

III Nylén, T., Luoto, M., 2015. Influence of patch size and connectivity on beach and dune species in land uplift coasts. (minor revision in Plant Ecology & Diversity)

IV Nylén, T., Luoto, M., 2015. Primary succession, disturbance and productivity drive complex species richness patterns on land uplift beaches. Journal of Vegetation Science 26, 267–277.

The publications are referred to in the text by their roman numerals.

Authors' contribution

The research plans were jointly made by T. Nylén and M. Luoto. All field work was designed, prepared and carried out by T. Nylén (Heidi Alanen assisted in the field). T. Nylén performed all pre-treatment of samples, laboratory analyses, data processing and statistical analyses. Peter C. le Roux supervised the statistical analyses of Paper II. Original versions of the manuscripts, including all tables, figures and photographs, were produced by T. Nylén. Manuscripts were then commented by all co-authors and edited by T. Nylén based on the comments.

Abbreviations

BRT	boosted regression tree
DEM	dynamic equilibrium model
GLM	generalised linear modelling; generalised linear models
GLMM	generalised linear mixed modelling; generalised linear mixed models
IDH	intermediate disturbance hypothesis
SGH	stress gradient hypothesis

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1 Introduction

1.1 The beach and dune habitat

Beaches and adjacent coastal dunes in the post-glacial land uplift area offer an excellent study setting for examining complex spatio-temporal processes (c.f. Kissling et al., 2012; Wisz et al., 2013). Specifically, beaches are characterised by dynamic environmental patterns that reflect the gradual shift in earth surface processes and they comprise extremely steep environmental gradients. Coasts subject to post-glacial rebound are extreme cases because pristine land emerges from the sea. Shoreline displacement leads to directional shifts in environmental patterns (Granö and Roto, 1989; Hellemaa, 1998).

Beaches support rather simple vegetation communities with relatively low total number of species (e.g. Moreno-Casasola, 1986; Maun, 2004; Forey et al., 2009). Nevertheless, beach vegetation is characterised by high species diversity within short distances. Primary biomass production, vegetation communities and species richness change rapidly along main environmental gradients and diversity is further increased by fine-scale heterogeneity (Fenu et al., 2013).

Beaches are harsh habitats and require specific adaptations to disturbance and stress, particularly sand movement, salt spray, ice scour, trampling, soil water scarcity and nutrient deficiency (Ranwell, 1972; Carter, 1988; Forey et al., 2008; Maun, 2009). The harsh environment is reflected in high degree of species specialisation (Chase, 2007). Beach specialists are mainly ruderals and stress-tolerators (universal adaptive strategy theory; Grime, 1979; Feagin and Wu, 2007). They tolerate disturbance and stress but are generally sensitive to competition (Ranwell, 1972; Maun, 2004; Feagin and Wu, 2007).

On account of the heterogeneous and specialised vegetation, beaches are recognised as important natural habitats (The Council of the European Communities, 1992; van der Maarel, 2003). Strong recreational land use pressures (e.g. van der Meulen and Udo de Haes, 1996; Martínez et al., 2006; Schlacher et al., 2014) make the understanding of the complex system vital for efficient conservation of beaches (Acosta et al., 2009; Álvarez-Molina et al., 2012).

Characteristically, key environmental gradients are strongly parallel along the shore-inland continuum. For example, site age (time since land emergence from the sea) and the intensity of earth surface processes are highly correlated although neither drives the other. Furthermore, primary biomass production is not solely controlled by substrate productive capacity but also by time and earth surface processes (Odum, 1969; Connell and Slatyer, 1977; McAtee and Drawe, 1980; Martínez and Moreno-Casasola, 1996; Martínez et al., 2001; Hesp et al., 2010; Levin et al., 2012; Zunzunegui et al., 2012; Brunbjerg et al., 2014).

As an attempt to solve multicollinearity problems caused by the parallel gradients, many studies have used elevation or distance from the shoreline as practical composite variables that combine the effects of multiple direct factors (review by Jutila, 1997). However, direct relationships cannot be tested with such approaches and potentially influential drivers may remain unregistered. Robust analyses of patterns and processes in beach systems require data that adequately quantify each environmental factor and modelling methods that are able to handle multicollinearity.

1.2 Beach and dune sediments along environmental gradients

The textural properties of the beach and dune sediments are assumed to be strongly interdependent (Folk and Ward, 1957; Hellemaa, 1998) and

to be largely controlled by geomorphic processes (Gerrard, 1981; Pye and Tsoar, 1990; Kasper-Zubillaga et al., 2007a, 2007b). Majority of studies document that increasing intensity of geomorphic processes leads to larger mean grain size, poorer sorting and coarse skewed and flatter grain size distributions (Friedman, 1961; Samsuddin, 1989; Pye and Tsoar, 1990; Arens et al., 2002; Kasper-Zubillaga et al., 2007a, 2007b; Poizot et al., 2013).

Individual studies, however, report contrasting effects (e.g. Fox et al., 1966; Bryant, 1982; Livingstone et al., 1999; Abuodha, 2003; Kim and Yu, 2009; Ergin et al., 2013; Van Oyen et al., 2013). For example Carter (1988) therefore concludes that grain size distributions are driven by site-specific rather than general processes. Several studies suggest that the effect of earth surface processes on sediment is masked by the strong influence of parent material (availability and primary properties of sand-sized sediments; e.g. Alestalo, 1971; Heikkinen and Tikkanen, 1987; Pye, 1991; Kasper-Zubillaga et al., 2007b, 2007c).

Organic matter is expected to accumulate in the soil with time (Salisbury, 1925; Burges and Drover, 1953; Barratt, 1962; Berendse, 1998; Berendse et al., 1998; Graham and Haynes, 2004). This effect is presumably one key mechanism of primary succession (Connell and Slatyer, 1977; Walker and del Moral, 2003; Stefansdottir et al., 2014). Organic matter accumulates particularly in sheltered zones along the shore-inland gradient (Gerrard, 1981; Kooijman and de Haan, 1995; DeBusk et al., 2005) and most rapidly in coasts sheltered from winds and waves (Incera et al., 2003; Rodil et al., 2007). Wet areas are suggested to have higher contents of organic matter in the soil than dry areas (Sevink, 1991).

1.3 Species diversity along environmental gradients

The dynamic equilibrium model (DEM; Huston, 1979, 1994; Kondoh, 2001) expands the intermediate disturbance hypothesis (IDH; Grime, 1973a; Connell, 1978) and the productivity-diversity hypotheses (Grime, 1973b, 1979; Tilman, 2004). DEM states that the interplay of disturbance and productivity determines the general patterns of species richness in all ecosystems (Huston, 1979). While disturbance (e.g. intensity of earth surface processes) has a detrimental effect on the survival of individuals, it decreases competition between individuals and species (Grime, 1973a; Huston, 1979). Similarly, productivity improves the survival chances of individuals but increases competition (Huston, 1979, 1994).

The level of disturbance that maximises species richness depends on the level of productivity: increasing disturbance is expected to lead to local extinction of species and decrease species richness in unproductive areas (Huston, 1979; Proulx and Mazumder, 1998; in dune systems e.g. Tahmasebi Kohyani et al., 2008; Brunbjerg et al., 2014). Disturbance is assumed to increase species richness in productive areas by creating competitor-free space and by increasing spatial heterogeneity (Huston, 1979; Proulx and Mazumder, 1998; Tahmasebi Kohyani et al., 2008; Plassmann et al., 2010; Brunbjerg et al., 2014). While DEM has wide empirical support, its simplicity and applicability have also received critique (e.g. Grace, 1999; Mittelbach et al., 2001; Gillman and Wright, 2006; Pärtel et al., 2007; Svensson et al., 2010; Graham and Duda, 2011). Further testing of the hypothesis with systematically collected data is called for (Whittaker, 2010; Fraser et al., 2014).

DEM (Huston, 1979, 1994) applies to a system with a strong temporal component because it

equals disturbance intensity with time from a major disturbance event (e.g. time since land emergence from the sea). Accordingly, time, disturbance and productivity are expected to be the key drivers of species richness in land uplift beaches (c.f. Tahmasebi Kohyani et al., 2008; Peyrat and Fichtner, 2011; Álvarez-Molina et al., 2012; Zuo et al., 2012; Brunbjerg et al., 2014). However, it is still insufficiently known how time interacts with disturbance and productivity in controlling species diversity.

1.4 Biotic interactions

Biotic interactions, particularly competition and facilitation, are assumed to strongly influence species distribution and richness (e.g. Connell and Slatyer, 1977; Callaway and Walker, 1997; Brooker and Callaghan, 1998; Davis et al., 1998; Gross, 2008, Cavieres and Badano, 2009). Competition and facilitation are expected to be reflected in species distribution as negative and positive associations, respectively, and they are presumably easily detected in ecosystems with low species richness and steep abiotic gradients (Kissling et al., 2012; le Roux et al., 2012; Wisz et al., 2013; le Roux et al., 2014).

The stress gradient hypothesis (SGH; Bertness and Callaway, 1994; Bertness and Hacker, 1994; Brooker and Callaghan, 1998) assumes that biotic interactions change from negative to positive along disturbance and stress gradients. Facilitation is suggested to drive primary succession in harsh ecosystems where pioneer species facilitate later colonists by modifying the environment (Connell and Slatyer, 1977). Many of these facilitative mechanisms involve changes in the substrate, including changes in organic, nutrient and soil moisture content (Whittaker, 1975; Connell and Slatyer, 1977) while other mechanisms are direct biological interactions between individuals (e.g. physical support and shade; Bertness and Callaway, 1994). In the favourable end of the disturbance gradient (or at late successional stage), many species are able to grow abundantly and competition is intense (Walker and Chapin, 1987; Brooker and Callaghan, 1998).

In line with the SGH, a dominance of facilitation over competition has been documented by a large number of studies in experimental settings (Vazquez et al., 1998; Franks and Peterson, 2003) and dune systems in tropical, subtropical (Franks, 2003; Martínez, 2003; Rudgers and Maron, 2003), temperate (Kellman and Kading, 1992; Lichter, 1998; Shumway, 2000; Armas and Pugnaire, 2009; Forey et al., 2009; Muñoz Vallés et al., 2011; Santoro et al., 2012) and subarctic climates (Gagné and Houle, 2001; Grau et al., 2010). Similarly, positive interactions have been shown to become more probable along the local disturbance gradient in dune systems (De Jong and Klinkhamer, 1988a, 1988b; Grau et al., 2010; Muhamed et al., 2013).

However, the SGH has rarely been tested with large observational datasets, multiple interacting species or in a setting where key abiotic factors have been taken into account. The conclusions may therefore be based on the responses of a few sensitive species or positive co-occurrences may result from shared habitat requirements (Maestre et al., 2005; Maestre et al., 2009; Meier et al., 2011; Kissling et al., 2012; le Roux et al., 2012). Furthermore, contradicting empirical evidence (e.g. Kadmon and Tielbörger, 1999; Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004; Grant et al., 2014) has led to a theoretical debate on the generality of the SGH (Maestre et al., 2005; Lortie and Callaway, 2006) and to formulation of extended models (Maestre et al., 2009; Doxford et al., 2013). Based on previous studies, positive associations of dominant and co-occurring species are expected to outweigh negative associations in harsh beach systems.

1.5 Influence of patch size and connectivity on vegetation

Beach habitats are naturally fragmented and unevenly distributed along the coastline and act as islands of suitable habitat for beach species (MacArthur and Wilson, 1963, 1967; Diamond, 1976; Obeso and Aedo, 1992; Bossuyt et al., 2003; Grainger et al., 2011). Therefore, the habitat pattern – size and connectivity of suitable habitat patches – is expected to influence the distribution and diversity of beach species (e.g. Diamond, 1976; Saunders et al., 1991; Margules and Pressey, 2000; Fischer and Lindenmayer, 2007; in dune systems Obeso and Aedo, 1992; Grootjans et al., 2001; Helm et al., 2006; del Moral et al., 2009). In some cases the effect of habitat pattern can outweigh the influence of local factors (Grainger et al., 2011).

Few studies have analysed the influence of habitat pattern on beach vegetation and those have focused on historical evidence of extinction and colonization (Obeso and Aedo, 1992) or a specific coastal zone (Bossuyt et al., 2003; Grainger et al., 2011). Observational data across the entire shore-inland gradient and accounting for key local factors (e.g. disturbance and productivity) is needed to advance the knowledge of the habitat pattern-local environment-vegetation relationship (c.f. Jacquemyn et al., 2001; Heikkinen et al., 2005; Raatikainen et al., 2009).

The island biogeography theory (MacArthur and Wilson, 1963, 1967) and metopopulation theory (Levins, 1969; Hanski, 1994, 1998) predict that patch size is reflected in population size and the probability of local extinction: largest patches have the potential to sustain highest diversity. Connectivity influences the probability of species colonisation and therefore well connected patches are expected to have largest number of species (MacArthur and Wilson, 1963, 1967; Debinski and Holt, 2000; Moilanen and Nieminen, 2002; Virtanen and Oksanen, 2007). The most exclusive species are assumed to be most vulnerable to habitat fragmentation (Hurme et al., 2007) while less site-selective species and species with efficient dispersal adaptations establish also in small, isolated patches (Tischendorf and Fahring, 2000; Grainger et al., 2011; Horsák et al., 2012; Driscoll et al., 2013).

Studies have suggested that patch size and connectivity moderate the site age-vegetation and productivity-vegetation relationships (Jacquemyn et al., 2001; Bossuyt et al., 2003; Horsák et al., 2012). The rate of successional vegetation changes is slower in isolated patches than in well-connected patches (del Moral et al., 2009). Consequently, large and well-connected patches may quickly become dominated by one competitor species while vegetation recovers slowly after disturbance in isolated patches (del Moral et al., 2009). Accordingly, habitat pattern is expected to influence the distribution and richness of beach specialists. Largest and best-connected patches presumably sustain highest number of specialist species.

1.6 Functional groups and adaptive strategies

Several studies suggest that instead of uniform responses, functional groups respond differently to environmental factors (Burns, 1997; Gould and Walker, 1999; Ingerpuu et al., 2003; Virtanen et al., 2013; in dune systems e.g. Isermann, 2011; Brunbjerg et al., 2014). Species adaptive strategies and biotic affiliations influence these responses. For example, ruderals are favoured by moderate disturbance because adaptations enable them to exploit the lack of competition (Grime, 1979; Kondoh, 2001; in dune systems Veer and Kooijman, 1997; Brunbjerg et al., 2014). Accordingly, the richness and abundance of beach specialists is expected to peak at an intermediate disturbance level while generalist species peak

at low disturbance levels.

The diverging responses may also arise from differences in growth form, size and root morphology (Jonasson, 1986; Choler, 2005; le Roux and Luoto, 2014). Moreover, the diversity of environmental responses has been suggested to be a prerequisite for the DEM and IDH (Petraitis et al., 1989; Dial and Roughgarden, 1998).

1.7 Aims of this study

The unique land uplift coasts, homogeneous observational data and advanced modelling methods provide an opportunity to robustly analyse environmental patterns and processes of the beach system (Wisz et al., 2013). The doctoral thesis aims at expanding on the knowledge of the beach and adjacent dunes as a complex ecogeomorphic system (i.e. biogeomorphic; e.g. Swanson, 1988; Levin, 1998; Hugenholtz and Wolfe, 2005; Stallins, 2006; Kim and Yu, 2009). The components of the system include the abiotic environment, substrate and vegetation together with geomorphic and ecologic processes that link them together (Fig. 1; e.g. Hugenholtz and Wolfe, 2005; Baas, 2007; Kim and Yu, 2009).

While beaches have received abundant attention from geomorphologists, sedimentologists and ecologists, many of the key processes are still insufficiently understood (Acosta et al., 2009; Álvarez-Molina et al., 2012). Furthermore, studies have mainly focused on distinct components of the system, rarely using the same study setting to simultaneously analyse geomorphic and ecologic processes (Stallins, 2006; Baas, 2007; Kim and Yu, 2009). Analyses mainly concentrate on a single zone of the beach system, apply traditional (often inflexible) modelling techniques or are based on small, heterogeneous or geographically limited datasets (Kim and Yu, 2009; Kissling et al., 2012; Wisz et al., 2013).

Current multidisciplinary research, ecogeomorphology, incorporates vegetation as simplified factors in landform-process simulations instead of accounting for the variety and dynamic nature of vegetation responses (Allen et al., 2014). Similar issues have complicated the incorporation of ecology also in other research fields (e.g. Collins et al., 2011; Smith et al., 2014).

This doctoral thesis analyses the individual components of the ecogeomorphic beach system (Fig. 1). Homogeneous transect survey data covering a wide geographical area (c. 60° N – 65° N) and appropriate modelling methods are utilised. The objective is to robustly test central hypotheses of geomorphology and ecology in a harsh and dynamic system. More specifically, the aims of the work are to answer:

(1) which abiotic, biotic and temporal factors are the main determinants of substrate (Paper I) and vegetation properties (Papers II and III),
(2) what are the effects of the main drivers on substrate (Paper I) and vegetation properties (Papers II, III and IV),
(3) how temporal processes interact with main spatial drivers in determining vegetation patterns (Paper IV) and
(4) how these effects differ between species and functional groups representing different adaptive strategies (Papers II, III and IV)?

The thesis utilises two advanced statistical methods, boosted regression tree (BRT) models and generalised linear mixed modelling (GLMM), to analyse the effects of multiple factors on substrate and vegetation. BRT models are capable of modelling complicated nonlinear relationships and interactions without *a priori* model specification and to robustly compare relative contributions of predictors (Friedman, 2001; Elith et al., 2008). GLMMs take the effect of lo-

cal environmental variability into account and potentially clarify general relationships; GLMM is therefore an efficient tool in hypothesis testing (Hox and Kreft, 1994; Bolker et al., 2009). Moreover, in Papers II and III, the effects of biotic and habitat pattern factors on vegetation are tested after carefully accounting for key abiotic factors (e.g. Meier et al., 2011; le Roux et al., 2012).

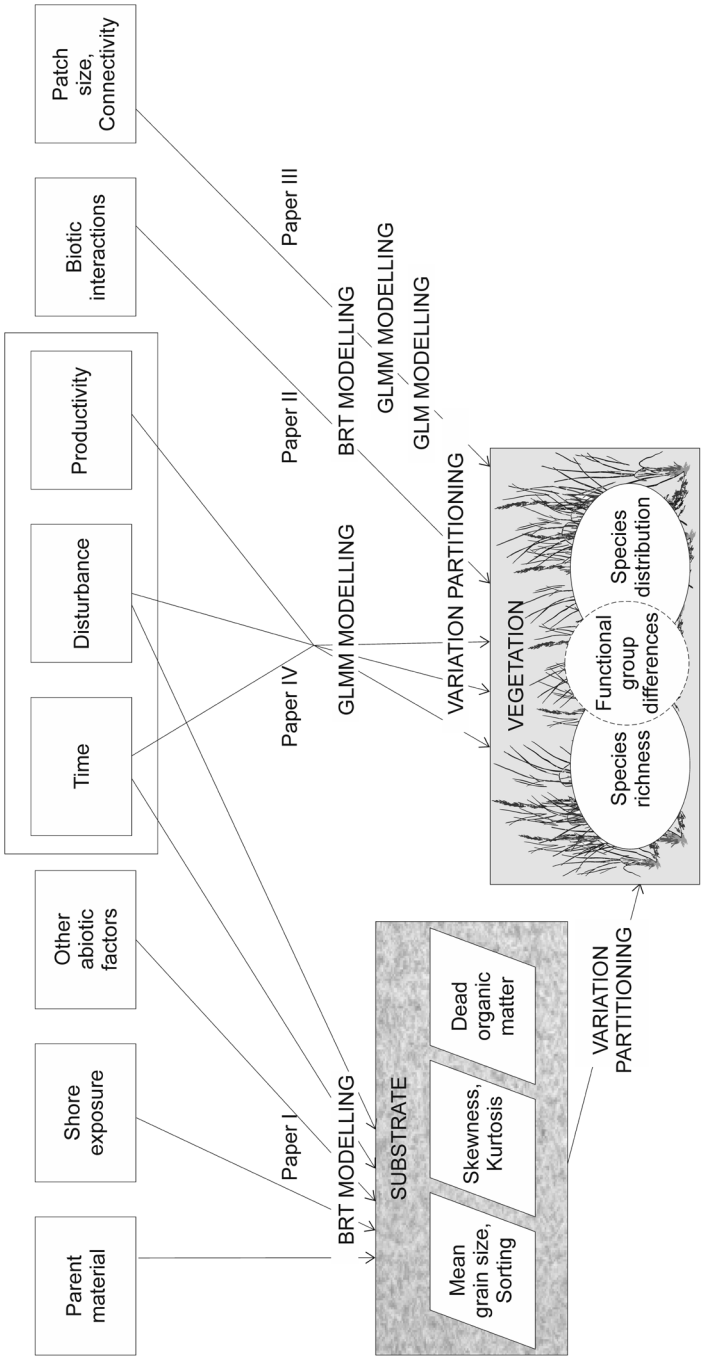


Figure 1. Schematic diagram of the beach system. The figure visualises those geomorphic, ecological and temporal processes that have been proposed in the literature and are tested in this doctoral thesis. In addition, the figure lists the utilised statistical methods and original papers where these links are tested. Variation partitioning is applied to assess the relative contributions of substrate, abiotic and habitat pattern factors on species richness in an analysis not included in the original papers. Time, disturbance and productivity are assumed (e.g. Huston, 1979; Proulx and Mazumder, 1998; Tahmasebi Kohyani et al., 2008; Brunbjerg et al., 2014) to be the key abiotic factors controlling vegetation.

2 Material and methods

2.1 Study area and sites

The data were gathered from the Finnish land-uplift coast of the Baltic Sea (Fig. 2). Open sand beaches and adjacent coastal dune fields were sampled, each beach and dune complex constituting one study site. All possible sites were identified from maps and aerial photographs of the National Survey of Finland. Based on a preliminary survey in summer 2010, 40 sites not severely degraded by eutrophication or recreational land use and with clear physical zonation were included in the study. Thus, the most active dune fields and, for example, public beaches were excluded from the survey. The minimum distance between individual sites was 200 meters.

The analyses in Papers I and IV were performed with 39 sites since the beach of Kallahti (developed on the steep flanks of an esker; Fig. 2) was excluded from the analyses due to divergent geomorphology. In a few cases two study sites constituted one continuous habitat patch because two transects had been surveyed in distant parts of the same large area of open sand. In Paper III 34 individual patches were therefore included in the study. The Kallahti site was excluded also from Paper III.

The selected study sites cover a large geographical area on the Baltic Sea coast (c. 60° N – 65° N; Fig. 2) and belong to the boreal vegetation zone (hemi-boreal – northern boreal; Ahti et al., 1968). Typical dune species include *Leymus arenarius*, *Honckenya peploides* and *Lathyrus japonicus* in the active white dune zone, *Deschampsia flexuosa* in the more stabilised grey dune zone and *Pinus sylvestris*, the dominant woody plant in forested dunes. The area is characterised by post-glacial land uplift resulting in rapid shoreline displacement and primary vegetation succession (Granö and Roto, 1989). Compared to oceanic coasts, wind speeds and waves are considerably lower in the Baltic Sea and yearly occurring sea ice acts as a geomorphic factor.

Sand beaches and adjacent coastal dune fields have a sporadic distribution in the study area (Fig. 2) and are typically small, isolated pockets. Large and well-connected sites are mostly associated with extensive glaciofluvial deposits (Fig. 2; Hellemaa, 1998). Individual sites included in the study had up to 600 kilometres between them which resulted in differences in climate, species pool, land uplift rate and availability of sand-sized sediments (Fig. 2). Moreover, differences in fetch, the distance wind passes over sea surface, varies considerably between sites (Fig. 2; Suominen et al., 2007).

2.2 Transect-based sampling of substrate, abiotic environment and vegetation

The field data were collected during a systematic fine-scale survey in the growing season of 2011. Southern sites were surveyed first (in mid-June) and northernmost sites last in order to time the sampling approximately for the peak of the growing season. At each site, one transect (14–122 meters long, depending on the width of the open sand area) was randomly placed. It started from the shoreline at coordinates that were randomly collected from the Topographic database of the National Land Survey of Finland (version 2010). The transect ran orthogonally through the open beach and dune area and ended in closed forest with full tree crown cover (Fig. 3).

The detailed profile of each transect was determined (measuring distance from the shoreline and absolute elevation) with an electro-optic distance meter and sampled at elevation intervals of 25 cm (both on upward and downward slopes; Fig. 3). The original data included 519 sampling points distributed along 40 transects. Analyses in Papers I, III and IV were run with 497 sam-

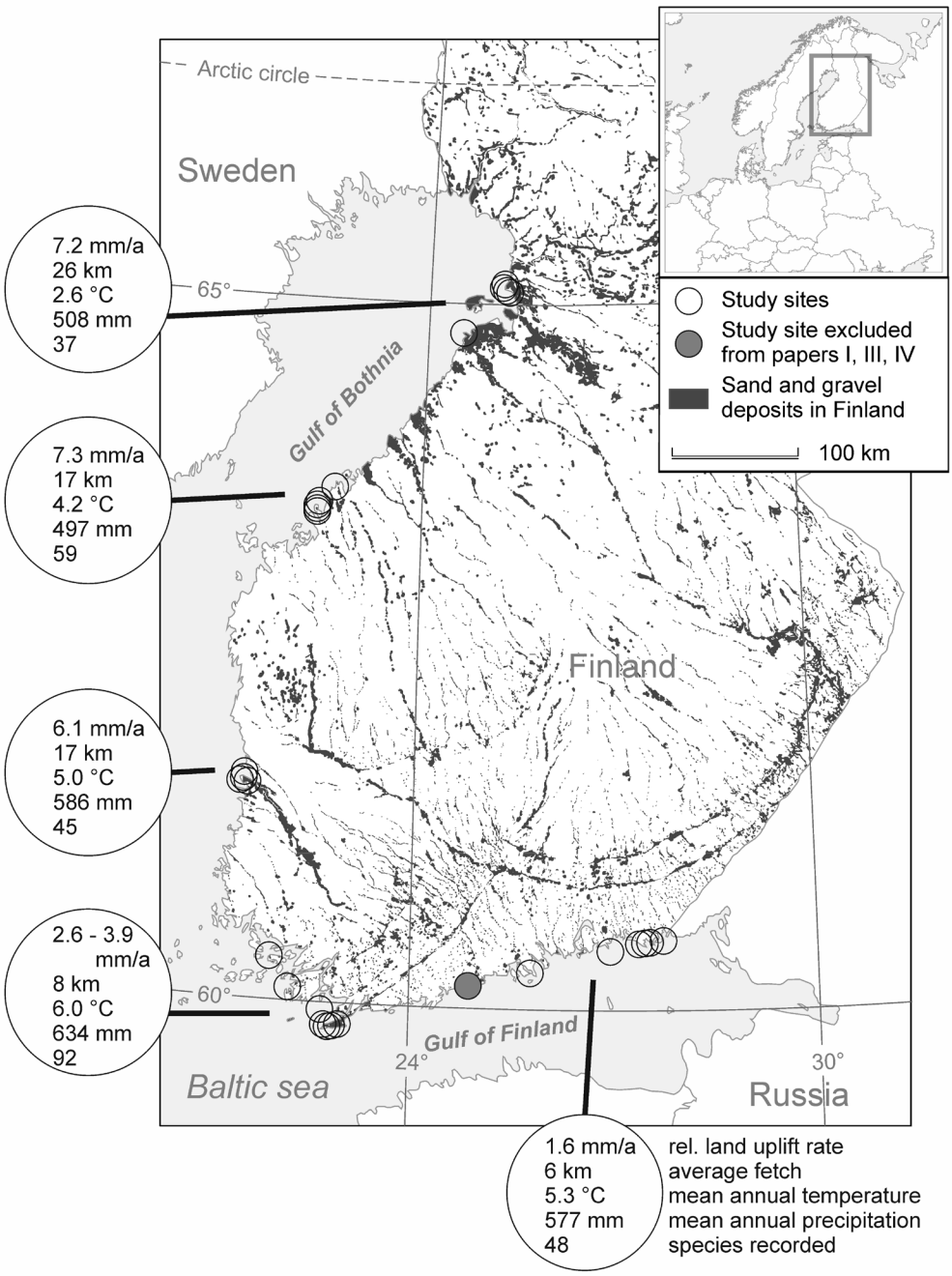


Figure 2. Locations of the study sites. Study sites are situated on the Finnish coast of the Baltic Sea and cover a wide geographical area (c. 60° N – 65° N, maximum distance 600 km). The distribution of sand and gravel deposits is presented (glaciofluvial and fluvial sediments; database of superficial deposits 1:20000 of the Geological Survey of Finland, edition 2013). The figure reports information on the relative land uplift rate (Johansson et al., 2004), average fetch (averaged over 48 directions and all study sites; Suominen et al., 2007), mean annual temperature, mean annual precipitation (Pirinen et al., 2012) and the total number of species recorded in this thesis in different parts of the geographical area.

pling points along 39 transects (or in 34 habitat patches). In each sampling point, geomorphological and other environmental variables were recorded, a sediment sample of 0.25 litres was collected from a depth of 5–10 cm and vegetation was surveyed in two adjacent square meter plots (2 x 1 m^2; Fig. 3).

2.3 Substrate and environmental data

In total, 506 intact sediment samples were analysed in the University of Helsinki laboratory of the Department of Geosciences and Geography. The samples were stored and pre-treated following standard procedures (ISO 11464). Two types of laboratory analyses were performed: first, subsamples were dry sieved following standard procedures (ISO/TS 17892-4; Roman-Sierra et al., 2013) and grain size parameters mean grain size, sorting, skewness and kurtosis were calculated with the Microsoft Excel add-in GRADISTAT using the geometric modified Folk and Ward (1957) graphical measures (Blott and Pye, 2001). Secondly, electrical conductivity (ISO 11265), soil organic matter (SOM) and soil moisture (SFS 3008) were measured following standard procedures. The percentage cover of the litter layer was visually estimated for each sampling point in the two adjacent square meter plots and averaged over the two plots.

Two main environmental variables were included in all analyses: site age (also called substrate age or succession time in original papers) and disturbance. Site age estimated time since a sampling point emerged from the sea. It was calculated from the relative land uplift rate of the nearest mareograph station (Johansson et al., 2004) based on the absolute elevation of the sampling point. Disturbance quantified the intensity of geomorphic processes. It was estimated as the percentage cover of ground dominated by signs of disturbance following the methodology of Hjort and Luoto (2009) and Virtanen et al. (2010). The estimation was based on signs of aeolian activity, wave-wash, ice-scour, flooding

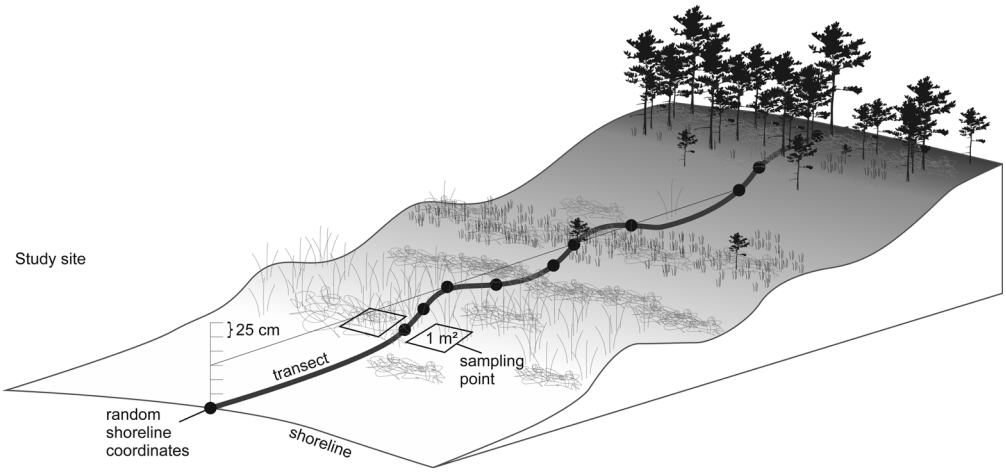


Figure 3. Schematic illustration of the sampling. At each study site, one transect was randomly placed. The transect ran orthogonally from the shoreline through the open beach and dune area towards inland. The transect ended in dune forest with full tree crown cover. Transect's profile was measured with an electro-optic distance meter and it was sampled at elevation intervals of 25 cm. In each sampling point, a sediment sample was collected, geomorphology and other environmental factors were recorded and vegetation was surveyed in two adjacent square meter plots (2 x 1 m^2). In the papers, vegetation parameters were either averaged or summed over these two adjacent plots.

and trampling (sand burial, dragging marks, exposed plant roots, damage and gaps in the vegetation, compaction of sediment, footprints, paths, tire tracks and walls of wave- and flood-wash materials; Hellemaa, 1998; Maun, 2004). Disturbance was consistently estimated by the same geomorphologist and litter cover by another observer to exclude variation resulting from observer differences and to ensure the independence of disturbance and litter data.

Further environmental and topographic variables included northing, local profile slope and curvature, open sand area, patch connectivity, fetch and ice period. Northing was determined as the north coordinate of the sampling point (ETRS89 coordinate system, horizontal accuracy of one meter) measured with a handheld GPS receiver. Local profile slope and curvature were calculated for each sampling point from the profile measurements based on three adjacent measurements. Curvature was calculated as the second derivative of a second order polynomial curve fitted into the three adjacent points on the profile.

Open sand area (i.e. patch size) was retrieved from a GIS database (Topographic database of the National Land Survey of Finland, edition 2013) and it measured the area of a continuous open sand surface. Patch connectivity was calculated from the same data following the methodology of Hanski (1994), Moilanen and Nieminen (2002) and Raatikainen et al. (2009). Fetch estimated the distance wind passes over open sea before reaching shoreline. For each transect, it was calculated in 48 directions and averaged over all directions (details in Suominen et al., 2007). Ice period was determined as the average duration of yearly sea ice period in the nearest ice observation station (Seinä and Peltola, 1991).

2.4 Vegetation data

In each square meter plot, I identified each vascular plant (nomenclature followed Hämet-Ahti et al., 1998), bryophyte (Koponen, 2000) and lichen (Stenroos et al., 2011) individual to species level. An exception were the few taxa that could not be reliably distinguished in the field or have changeable taxonomy (*Taraxacum* spp., *Cladonia* spp., *Hypogymnia* spp.; Hämet-Ahti et al., 1998). *Festuca rubra* ssp. *arctica* was identified to subspecies level since it is the only subspecies occurring in beach and dune environments (Hämet-Ahti et al., 1998). However, all identified taxa are later referred to as "species". The horizontal percentual cover of each species was estimated allowing the sum of cover values to exceed 100 % (layered vegetation).

Five species were identified as dominant based on that they were present in over 15 % of the sampling points or covered at least 4 % of the sampled area: *Leymus arenarius* (tall grass, present in 43 % of the sampling points and covering 11 % of the sampled area), *Honckenya peploides* (succulent forb, 22 % and 5 %), *Pinus sylvestris* (evergreen tree, 17 % and 10 %), *Lathyrus japonicus* (legume, 17 % and 3 %) and *Deschampsia flexuosa* (grass, 13 % and 4 %). In addition, the total dominant cover was calculated as the sum of all five dominant species covers. Dominant species were used as proxies for the intensity of biotic interactions (le Roux et al., 2012).

Four types of variables were derived from the species cover observations. Firstly, species were placed in functional groups for group-wise examination. Broadly, species were grouped to vascular and cryptogam species (Paper II) and more specifically based on taxon and growth form following a widely used classification (e.g. Chapin et al., 1996; Bruun et al., 2006; Paper IV). I recorded in total 14 woody plant and shrub, seven dwarf shrub, 62 forb, 22 graminoid, eight bryo-

phyte and five lichen species (based on 39 study sites). Of all recorded species, 11 grow exclusively on sandy beaches in Finland (Hämet-Ahti et al., 1998; Lampinen et al., 2014) and they formed an additional functional group of beach specialists (Papers III and IV). Secondly, species cover values were converted to binary presence/absence data for species distribution modelling. Thirdly, total and functional group species richness was calculated as the number of species present in the plot.

Fourth, the sum cover of herbaceous vascular plant species in each plot was calculated and used as a proxy for annual primary production of biomass or "productivity" in further modelling. This was considered as a non-destructive and efficient estimation method for four reasons: the fragile vegetation cover was not removed or damaged, the survey found herbaceous vascular plants in 369 out of 379 vegetated sampling points (based on 39 transects), 95 % of the annual biomass production may be produced by graminoids (Dilustro and Day, 1997) and the studied environmental, vegetation cover and biomass gradients are extremely steep (Pollock et al., 1998; Grytnes, 2000; Röttgermann et al., 2000; Mittelbach et al., 2001; Krebs et al., 2003; Muukkonen et al., 2006). Furthermore, it has been shown that species richness is more directly related to the light penetration to the soil surface (accurately estimated by vegetation cover variables) than to other productivity measures (Tilman, 1993; Grace and Pugesek, 1997; Kull and Aan, 1997; Grace, 1999).

2.5 Modelling methods

To analyse the response of substrate and vegetation properties to environmental factors, two modern statistical modelling techniques were utilised: boosted regression tree models (BRT; Friedman, 2001; Elith et al., 2008) and generalised linear mixed modelling (GLMM; Hox and Kreft, 1994; Bolker et al., 2009). BRT modelling was applied to identify the main determinants of multiple substrate properties and to analyse their individual effects (Paper I). The tested predictor variables included northing, elevation, distance from the shoreline, profile slope, profile curvature, site age, disturbance, open sand area, submergence probability, fetch, yearly average sea ice period, soil moisture content and electrical conductivity. In addition, BRT models were used to analyse the effects of biotic factors (dominant species covers; Paper II) and habitat pattern (patch size and connectivity; Paper III) on species distribution and richness, and to compare their influence to the contribution of abiotic factors (site age, disturbance and productivity).

BRT modelling combines statistical and machine learning traditions to fit a large number of simple models (decision trees; De'ath and Fabricius, 2000) to the data and uses boosting to combine the simple models. Consequently, it constructs a prediction without *a priori* specification of the data model and reproduces complex non-linear relationships and interactions (Elith et al., 2008). The relative contributions of each predictor variable in a BRT model were calculated from the reduction of squared error attributable to each variable, averaged over all trees and normalised to sum up to 100 (Friedman, 2001). Partial dependence functions were plotted to visualise the dependency between fitted response and an individual predictor, after integrating out the effects of all other predictors (Friedman, 2001).

GLMM was used to model the interactive effects of site age, disturbance and productivity on total and functional group species richness (Paper IV). In addition, GLMM was used to reanalyse the effects of habitat pattern (patch size and connectivity; Paper III) on species distribution and richness. The analyses in Paper III were repeated with a third method, generalised linear

modelling (GLM) to ensure that the results are independent of selected method. GLMM is a generalised regression method that handles response variables with non-normal error distributions and in addition to fixed effects takes into account the random effects of repeated measures on the same statistical units (Hox and Kreft, 1994; Bolker et al., 2009). GLMM was selected as an appropriate method for hypothesis testing since it can take into account the effects of environmental variability in a spatially clustered data. GLMM is particularly useful in testing theoretically established models with strong assumptions of the independent and interactive effects. Moreover, I was particularly interested in interactive effects that are parameterised and can readily be quantified and visualised with GLMM.

Variation partitioning (Borcard et al., 1992; Liu, 1997; Anderson and Gribble, 1998) was applied to examine the relative importance of three predictor groups, main abiotic factors (site age, disturbance and productivity), substrate factors and habitat pattern factors, in determining species richness. Total and specialist species richness were modelled individually. Full (including all predictor groups) and partial (all unique single- and two-group combinations of the predictor groups) BRT models were fitted into the data. Following Heikkinen et al. (2004), unique and joint contributions of the predictor groups were calculated based on deviance explained in different combination models. Ten-fold cross-validation with random assignment (Fielding and Bell, 1997) was used to determine the residual deviance. Relative contributions of individual predictors in full models were then examined (Friedman, 2001). Model settings were kept identical to the analyses in original publications (Papers I, II and III).

2.6 Model validation and evaluation

In BRT modelling, ten-fold cross-validation with random assignment was applied to develop (select optimal settings to minimise predictive error) and evaluate the model (Fielding and Bell, 1997; Elith et al., 2008). The data were randomly divided into ten subsets, and ten unique training sets, each omitting one subset, were constructed. In each of the ten cross-validation folds, the model was built with one training set and tested against the withheld validation data to identify the optimum number of decision trees. The inference in BRT modelling and standard regression have fundamental differences: in BRT modelling selecting the optimum settings and examining the relative contribution of predictor variables are analogous to variable selection and significance testing (Friedman, 2001; Elith et al., 2008).

When the optimum settings and the best BRT model had been selected, a cross-validation correlation (Spearman rank correlation of model prediction and validation dataset observations) was calculated as a measure of model performance in the analyses of substrate properties (Paper I) and species richness (Papers II and III). In the species distribution analyses (Papers II and III), predictions were converted to binary presence/absence data using a species-specific threshold that maximized model specificity and sensitivity (see le Roux et al., 2013 for details). These predictions were compared to observations in the validation dataset with the area under curve of a receiver operating characteristic plot (AUC; Fielding and Bell, 1997) to estimate model performance.

In Paper III, best GLMMs and GLMs were selected based on Akaike information criterion value (AIC) and model fit was evaluated based on AUC (occurrence variables) and Spearman rank correlation between observations and predictions (richness variables). For GLMMs in Pa-

per IV, the Wald Z statistic and associated p-value were calculated to weigh the significance of fixed terms (Bolker et al., 2009). The Wald Z statistic is a traditional significance testing tool in mixed modelling. Non-significant terms were removed from the model with backward elimination. Spatial autocorrelation of response variables was examined by calculating Moran's I. There was no significant ($p < 0.01$) spatial autocorrelation in the original data and fitting the BRT models significantly decreased the values of Moran's I (calculated for model residuals).

3 Results and discussion

3.1 Paper I: Main determinants of substrate properties

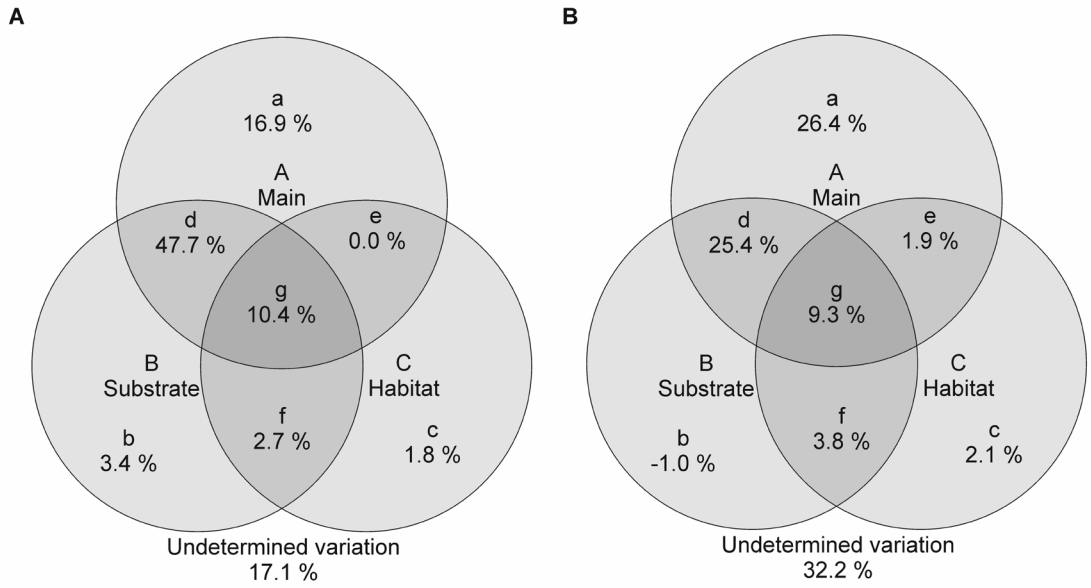
The analysis was able to identify the main determinants of mean grain size, sorting and organic properties of the substrate in the beach system. On the contrary, skewness and kurtosis of the grain size distribution are to a large extent controlled by unmeasured or stochastic processes. I suggest that skewness and kurtosis are strongly influenced by the geomorphological origin of the sediment. As expected (e.g. Alestalo, 1971; Heikkinen and Tikkanen, 1987; Pye, 1991; Kasper-Zubillaga et al., 2007b, 2007c), the analyses indicate a strong influence of parent material. This may be an effect specific to relatively low-energy systems where waves and winds inefficiently sort and transport parent materials (Hellemaa, 1998).

Based on the results, mean grain size and sorting are highly interdependent (Folk and Ward, 1957; but see Ergin et al., 2013; Van Oyen et al., 2013) and are influenced by the exposure (to winds and waves) of the beach (e.g. Folk and Ward, 1957; Arens et al., 2002). Interestingly (Folk and Ward, 1957; Friedman, 1961; Fox et al., 1966; Pye and Tsoar, 1990; Arens et al., 2002), the results indicate that grain size decreases and sorting improves along the exposure gradient, potentially due to insufficient sorting processes (c.f. Bryant, 1982). As expected, the intensity of geomorphic processes determines organic matter content in the soil and in the litter layer (Gerrard, 1981; Hellemaa, 1998; DeBusk et al., 2005). Increasing disturbance generally slows down the accumulation of organic matter (Gerrard, 1981; Kooijman and de Haan, 1995; DeBusk et al., 2005). The results suggest that, whereas the cover of litter layer is mainly controlled by the transient intensity of geomorphic processes, the slower process of soil organic matter accumulation is also strongly influenced by the exposure of the coast.

3.2 Main determinants of vegetation

Variation partitioning identified the main factors – site age, disturbance and productivity – as the predictor group with highest unique contribution in total species richness and specialist richness models (Fig. 4). Disturbance was identified as the one most influential variable in predicting total species richness (da Silva et al., 2008; Houle, 2008; Tahmasebi Kohyani et al., 2008; Gornish and Miller, 2010; Brunbjerg et al., 2014) while specialist richness was closely related to productivity (Fig. 4). These results highlight the importance of accounting for the effects of time, disturbance and productivity in diversity modelling (Papers II and III; e.g. Meier et al., 2011; le Roux et al., 2012).

While substrate and habitat factors had negligible unique contributions, the joint contributions of particularly the main abiotic and substrate factors (Maun, 2004, 2009; Frederiksen et al., 2006; Forey et al., 2008) and, to some extent, of all predictor groups were notable (Fig. 4). Soil organic matter and litter layer cover were detected as influential factors in species richness mod-



C

Predictor (group)	Relative contribution, % (model ABC) Total	Specialist
Disturbance (A)	41	4
SOM (B)	18	14
Productivity (A)	13	41
Litter cover (B)	8	2
Connectivity (C)	4	11
Skewness (B)	4	4
Site age (A)	3	7
Kurtosis (B)	3	4
Sorting (B)	2	2
Mean grain size (B)	2	7
Patch area (C)	1	3

Figure 4. Results of the variation partitioning analysis for (A) total species richness and (B) specialist richness. The figure reports the fractions of deviance explained by three groups of predictors: main abiotic predictors and time A, substrate predictors B and habitat pattern predictors C. Both unique (a, b, c) and joint contributions (d, e, f) of predictor groups on richness variables are determined based on deviance explained (estimated with cross-validation). In addition, the relative contributions of individual predictors on species richness are reported (C) based on the ABC-model (BRT model including all predictor groups).

els (Fig. 4; e.g. Tilman, 1993; Hellemaa, 1998; Houle, 2008; Fenu et al., 2013; Brantley et al., 2014). Indeed, in addition to abiotic factors, biotic processes cause changes in the substrate, including changes in organic, nutrient and soil moisture content which in turn affects vegetation patterns (Whittaker, 1975; Connell and Slatyer, 1977). This result suggests that there is a need for further research on the two-way soil organic material-vegetation relationship, potentially with such data as produced in this thesis.

This analysis suggests that textural properties do not have important effects on vegetation (see however Fenu et al., 2013; Brantley et al., 2014). As expected (Paper III; Saunders et al., 1991; Obeso and Aedo, 1992; Margules and Pressey, 2000; Fischer and Lindenmayer, 2007), connectivity influences specialist richness and its effect is comparable to key abiotic and substrate factors (Fig. 4). Furthermore, variation partitioning results indicated that a large part of variation in specialist richness remains undetermined even when an extensive set of factors (except for biotic) are taken into account (Fig. 4). Most of this remaining variation is potentially explained by biotic interactions (Paper II).

3.3 Paper II: The influence of biotic interactions on vegetation

The results show that including biotic interactions significantly improves species distribution and richness models for coastal beach systems even when key abiotic factors and geographical differences are accounted for. Expectedly (e.g. Connell and Slatyer, 1977; Brooker and Callaghan, 1998; Franks and Peterson, 2003; Martínez et al., 2004; Grau et al., 2010), biotic interactions are identified as important drivers of beach and dune vegetation patterns at three organisation level: the entire community, functional groups and individual species. Some of the biotic variables are as influential as key abiotic factors (time, disturbance and productivity) in predicting vegetation patterns.

Based on the SGH, positive biotic interactions were expected to dominate over negative interactions in harsh, dynamic ecosystems (e.g. Bertness and Hacker, 1994; Brooker and Callaghan, 1998; Franks and Peterson, 2003; Forey et al., 2009; Grau et al., 2010). However, this study found no dominance of either positive or negative co-occurrences in boreal beach and dune systems (Kadmon and Tielbörger, 1999; Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004). This is in line with the more recent ideas of some researches (Maestre et al., 2005, 2009; Doxford et al., 2013) who argue that the SGH does not generally apply to all species or habitats or at all times.

The results of this study suggest that taxonomic groups (vascular plants and cryptogams) and individual species have idiosyncratic instead of uniform responses to the presence of dominant species (Tielbörger and Kadmon, 2000; Maestre et al., 2009; le Roux et al., 2012; Arfin Khan et al., 2014; Grant et al., 2014). Moreover, there is strong evidence of divergent responses to individual dominant species. The differences between vascular plants and cryptogams and with different dominant species probably result from differences in size, life form, life stage, physiology and adaptive strategies (c.f. Kellman and Kading, 1992; review by Callaway and Walker, 1997; Maestre et al., 2009). The analysis thus shows that dominant species have an important role in shaping vegetation assemblages and may further indirectly influence the beach and dune landscape.

3.4 Paper III: The influence of patch size and connectivity on vegetation

The study demonstrates that patch size and connectivity significantly improve predictions of beach species distribution and richness in land

uplift coasts. The influence of the habitat pattern is comparable to the effects of key local drivers and time (site age, disturbance, productivity; c.f. Raatikainen et al., 2009). The results are similar over three modelling methods indicating that the effects are independent of the selected statistical method. Thus, the habitat pattern strongly influences the diversity and distribution of habitat specialists in beaches and dunes (c.f. Saunders et al., 1991; Obeso and Aedo, 1992; Margules and Pressey, 2000; Fischer and Lindenmayer, 2007). The influence is stronger than expected because beach and dune specialists have efficient long-distance dispersal mechanisms (review by Maun, 2009). This was expected to make them less dependent on the habitat pattern.

Unexpectedly (Obeso and Aedo, 1992; Debinski and Holt, 2000; Bossuyt et al., 2003; Hurme et al., 2007; Virtanen and Oksanen, 2007; Grainger et al., 2011), patch size and connectivity do not have uniform positive effects on the probability of species occupation or on species richness (c.f. Harrison, 1997; Scheffer et al., 2006). Instead of uniform impacts, the results highlight species-specific dependence on the habitat pattern (c.f. Raatikainen et al., 2009; Gallego-Fernández et al., 2011). As expected (e.g. Gallego-Fernández et al., 2011; Grainger et al., 2011; Horsák et al., 2012), total species richness is less influenced by patch size and connectivity than exclusive specialist richness. The open patches act as distinct habitat islands only for exclusive specialists while the majority of the flora may inhabit also the dry dune forests and heaths surrounding the patches (e.g. Tischendorf and Fahrig, 2000; Devictor et al., 2008; Driscoll et al., 2013). Total richness is highest in small patches that may be more easily invaded by generalist species (Harrison, 1999) and both in relatively isolated and well-connected patches. This analysis demonstrates that both the habitat patch network and local environmental conditions should be accounted for to efficiently protect beach species.

3.5 Paper IV: Interplay of main factors controls species richness

The analysis demonstrates that the effects of time, disturbance and productivity on species richness are strongly interactive in coastal beach systems. When site age and productivity increase, competitive exclusion becomes intense and disturbance starts to favour diversity by opening up competitor-free space (Maun, 2004; Tahmasebi Kohyani et al., 2008; Plassmann et al., 2010). While species richness is at young sites minimised by intense disturbance and low productivity, maximum species richness occurs at old sites where both disturbance and productivity are low. These results are in line with the DEM (Huston, 1979; Kondoh, 2001; in dune systems e.g. Tahmasebi Kohyani et al., 2008).

Diverging environmental conditions favour the richness of different functional groups (e.g. Isermann, 2011; Brunbjerg et al., 2014). The habitat specialist group benefits from shorter site age and more intense disturbance than groups consisting of generalist species (Veer and Kooijman, 1997; Forey et al., 2009; Brunbjerg et al., 2014). They are therefore able to take advantage of productive aeolian sands. Thus, the heterogeneous species richness patterns of the beach habitat are created by the interplay of key environmental factors and the functional groups' diverging responses. Furthermore, areas with intense geomorphic processes may have an important role in sustaining the diversity of habitat specialists (e.g. Aptroot et al., 2007; Brunbjerg et al., 2014).

3.6 Implications for future research

To further deepen the understanding of the land uplift beach system, future research should address three relationships in detail: the influence of vegetation on geomorphic processes (e.g. Bendix

and Hupp, 2000; Baas, 2007), on productivity and on substrate properties (Fig. 5; Jenny, 1958; Moro et al., 1997; Muñoz Vallés et al., 2011). Thus, the next steps for the multidisciplinary beach research may include: 1) further research on individual (multidirectional) links and 2) refining the conceptual model of the system potentially utilising such methods as structural equation modelling (e.g. Fox, 1980; Graham, 2003).

Future research should also examine if the results of this work are specific to the Baltic environment. Does the Baltic Sea, for example, merely represent one end of an exposure gradient or does the relatively small species pool considerably alter general ecological processes? Are the results transferable to other types of disturbance-driven ecosystems? As an example, the exposure-grain size relationship revealed by this thesis – opposite to previous findings from oceanic environments – could indicate that the true relationship is U-shaped.

Expanding the homogeneous observational dataset and utilising appropriate statistical methods following the guidelines of this thesis would be a good approach to disentangling the remaining issues. Incorporating experimental data would further strengthen the interpretation of causal processes. One important goal shoud be to integrate the results of recent research with conservation planning.

4 Conclusions

In this work, I was able to test many of the links of the ecogeomorphic beach system by assessing the validity of established assumptions. Key geomorphic and ecologic processes that control multiple substrate and vegetation properties were tested and analysed. This was achieved using appropriate statistical methods and extensive observational data covering the entire gradient from shoreline to dune forest and a wide geographical area. The main conclusions drawn from the study can be summarized in a following way:

- (Aim 1) Parent material, i.e. the availability of sand and its primary properties, in combination with shore exposure largely control textural properties of the beach substrate (Fig. 5). Shore exposure and the local intensity of geomorphic processes dictate organic properties of the substrate (Fig. 5). Time does not have a clear effect on substrate, but it strongly influences vegetation properties. Time, disturbance and productivity in concert with biotic interactions determine the distribution of species and species richness (Fig. 5). Particularly, dominant species have an important role in shaping species distribution and richness patterns. They may therefore notably influence the evolution of beach and dune landscapes.

- (Aims 2 and 3) Shore exposure and disturbance have negative effects on the accumulation of organic matter and increasing exposure leads to smaller grain size and better sorting. As predicted by the DEM, the effects of time, disturbance and productivity on species richness are highly interactive. Increasing site age and productivity have initially positive effects on diversity but unless disturbance creates competitor-free space, improving habitat conditions lead to intense competition and diversity loss. The level of productivity that maximises diversity thus depends on site age and disturbance. There are both positive and negative species co-occurrences in these beach systems and, unexpectedly, positive biotic interactions do not dominate over the negative ones (Fig. 5).

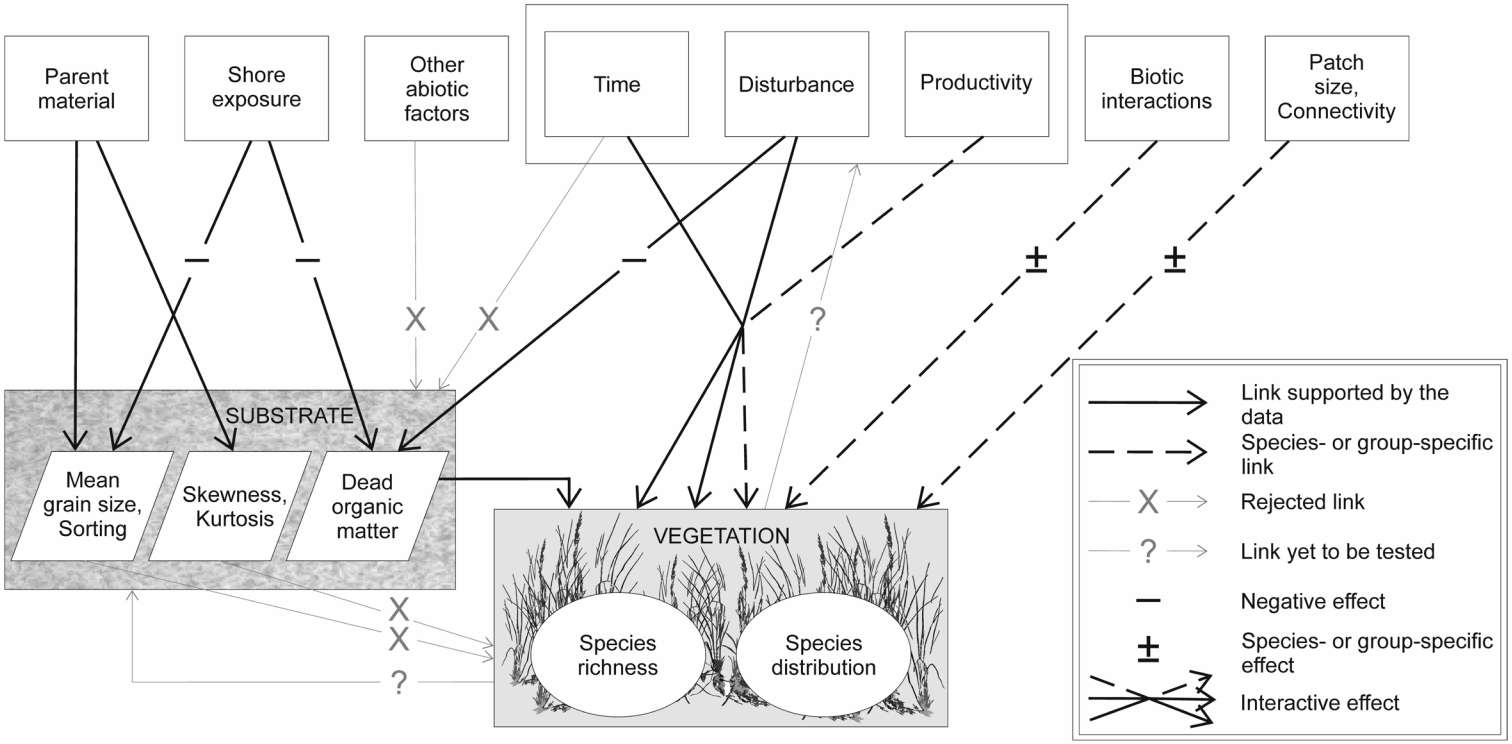


Figure 5. Conceptual diagram of the beach system with key results of the doctoral thesis. The figure identifies the abiotic, biotic and temporal factors whose effects on substrate and vegetation have been proposed in literature and were tested in the analyses. The figure differentiates between the supported general links, supported but species- or group-specific links and rejected links. The detected negative effects, taxon-specific effects and interactive effects are illustrated. In addition, effects yet to be tested are shown.

- (Aim 4) Individual species and functional groups have divergent responses to abiotic and habitat pattern factors and different biotic interactions. The disturbance-tolerant habitat specialists are more diverse at an intermediate successional stage and at intermediate levels of disturbance and are therefore able to take advantage of the fresh, productive aeolian sands. Beach and dune patches act as islands of suitable habitat for specialists and therefore strongly influence their distribution and richness (Fig. 5). These patches are at the range margins of the generalist species. Therefore, generalists thrive at low levels of disturbance at late successional stages and are not affected by the size or isolation of the patch. Moreover, biotic interactions are species- and functional group -specific even in harsh dynamic environments (Fig. 5).

Thus, this study expands on multiple geomorphic, ecologic and temporal components of the beach system (Fig. 5). It may be regarded as one step towards unifying the knowledge of the complex environment-substrate-vegetation system on land uplift beaches in the spirit of ecogeomorphology. Recent studies point out that existing ecogeomorphology research largely ignores the complex ecological processes and the diversity of vegetation responses. Before these can be implemented into ecogeomorphic models, robust and detailed ecological knowledge must exist.

I suggest that these challenges should be addressed by acquiring large homogeneous data, merging observational and experimental approaches and utilising advanced statistical methods. The thesis introduces guidelines for observational data acquisition and analysis. Furthermore, the results of this thesis and other recent research should in future be built into diversity and species distribution models that guide decision making in conservation planning.

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